THE UTILIZATION OF SUGARS AND OTHER SUBSTANCES BY DROSOPHILA

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Studies have been made of the use of carbohydrates and other food material by several insects, e.g. the honey-bee (Bertholf, 1927; Phillips, 1927; Vogel, 1931), the blow-fly (Fraenkel, 1936, 1940), the Mexican fruit fly, *Anastrepha ludens* (Baker et al., 1944), and a number of others. The reviews of Trager, 1941 and 1947, and Uvarov, 1928, furnish extensive references. *Drosophila melanogaster* seems, however, to have escaped attention in this connection heretofore. Experiments have now been made on the ability of this fly to utilize a large number of carbohydrates and related compounds, as well as some substances of other classes. In addition, an estimate of the relative nutritional efficiency of these substances has been made.

Material and Methods

Adults. To rear flies for these tests, the standard corn meal, agar, and sugar medium, in half-pint milk bottles, with an inoculation of fresh yeast, was used. As soon as the larvae reached full size and began to leave the medium, a layer of sawdust was added. This prevented the adults from obtaining any food until they were transferred to test bottles. The flies were used as soon as possible, never more than 24 hours after emergence.

Test bottles were set up as follows: solutions to be tested were put into 10 ml. vials stoppered with a roll of filter paper which served as a wick. About 50 ml. of 1.5 per cent agar was poured into a half-pint milk bottle: this maintained moisture and facilitated counting dead flies. For non-fermentable substances the vials were simply embedded in the agar base, otherwise they were wrapped in strips of paper toweling to form a plug for the milk bottle. This stopper could be changed readily and fresh solutions offered the flies, eliminating the complications of bacterial growth. It was found desirable to transfer the flies to fresh bottles after about two weeks if they survived, since otherwise dead flies were eaten by larvae and counting became difficult.

One hundred flies were used for each test. They were divided among three bottles for convenience in counting. The dead flies in the bottles were counted each day. Initially the number of days required for 50 per cent of the flies to die was used as a means of evaluating the degree of utilization of a substance, but it was found that many of the materials having low values could not be differentiated without making counts at shorter intervals, which was impractical. A better index was achieved by totalling the daily survival percentages and using the resulting number as an index of nutritive value. For example, when formic acid was fed to flies, all survived the first day, 43 per cent the second, none the third. The "score" was, therefore, 143.

Larvae. Three of the common sugars were tested on sterile larvae. Eggs were obtained by allowing flies to deposit them on small dishes of agar for about two hours; the eggs were then collected and sterilized by immersion in 85 per cent alcohol for 10 minutes and transferred to shell vials containing 10 ml. of sterile culture medium. Each vial contained the following: powdered agar, 150 mg.; dried brewer's yeast, 50 mg.; sugar, 50 mg.; distilled water, 10 ml. The same medium, minus sugar, is the "starvation diet" of Beadle et al. (1938), and this, together with their "adequate" diet of 2 per cent yeast, was used for comparison with the sugar supplemented media.

Each vial was seeded with 40 eggs and maintained at 25° C. After the formation of pupae, the vials were examined daily and when all the adults had emerged, counts were made to ascertain: (a) number of adults; (b) number of pupae not completing metamorphosis; (c) number of unhatched eggs. The larvae sometimes churned the medium so that unhatched eggs were lost, but a large number of vials were found with eggs and egg cases undisturbed; from these it was calculated that an average of 4 eggs per vial failed to hatch. The numbers of eggs given in Table IV represent, therefore, 36 eggs per vial.

Results

If flies are put into dry bottles, they are all dead within 48 hours: their score is 65. If a layer of agar is put into the bottles, the score is 110; if, in addition, a vial of distilled water is supplied, the score rises to 120. On standard corn meal, agar, and sugar medium, they live a long time: the score for that is 4418.

Table I shows the scores calculated as described above, and the day on which 50 per cent of the flies in each test were left alive. From the data it can be seen that adults of *Drosophila melanogaster* can live on a large number of substances in several classes of chemical compounds, but that the sugars and their close derivatives are best for maintaining these insects. Even in the sugars, each subgroup is found to contain substances which cannot be utilized.

If flies are supplied with pure sugar solutions, they survive for periods dependent upon the degree of utilization of the sugar and its concentration. Poorly utilized sugars like xylose sustain life only for short periods, even in concentrated solutions, while well utilized sugars like sucrose maintain life for longer and longer periods as the concentration increases. The limit in this direction seems to be reached between M/10 and M/5 for sucrose, for further increases in the concentration fail to increase survival. Groups of flies tested with concentrations of sucrose as follows: M/5, M/2, M, and 2M gave results no better than M/10, and indeed, the higher concentrations showed a tendency to decrease the life span slightly, but other factors such as osmotic pressure might enter to account for this.

The substances which were tested gave scores ranging from that of raffinose, 2600, to guanine, 13, as shown in Table I. Three groups of substances can be distinguished:

Group 1. Substances which appear to be inert, with scores close to that of water. Because of the natural variability of different batches of flies, and temperature conditions as noted previously, one could not expect sharply demarcated groups, and in fact there is a continuous gradation of scores. Probably all substances with scores between 100 and 150 should be called inert. This group would

Table I

The survival of adult Drosophila melanogaster on various substances, given as summations of daily survival percentages (A), and as days required for 50 per cent mortality (B). Except where noted, solutions are M/10. Each test represents 100 flies.

	A	B		A	B		A	B
Controls			Trisaccharides			Carboxylic acids		
Dry bottle	65	1	Raffinose	2600	28	Butyric	205	3
Bottle with agar	110	2	Melezitose	2432	26	Acetic	202	3
Water (442 flies)	120	2	Raffinose, M/20	1460	15	Formic	143	2
Standard medium	4418	45	Melezitose, M/20	909	14	Valeric	133	2
						Propionic	113	2
Pentoses			Polysaccharides			Lactic, M/2	377	5
						M/5	327	4
D-Xylose, M/2	680	7	Dextrin, 1%	778	8	M/10	208	3
Ribose	340	4	Starch, 1%	334	4	M/20	153	2
D-Xylose	211	3	Glycogen, 1%	298	4	Pyruvic, M/5	100	2
L-Fucose	169	3	Inulin, sat. sol.	160	2	M/10	90	2
D-Arabinose	166	3				M/20	75	2
D-Xylose, M/20	131	2	Alcohols			Glycolic	107	2
L-Arabinose, M/2	101	2				Levulinic	97	2
L-Rhamnose, M	80	2	Ethyl, M/5	172	3	Succinic	367	4
D-Arabinose, M/2	69	2	Ethyl, M/2	99	2	Pimelic	160	3
L-Rhamnose	68	2	Ethyl, M/10	93	2	Glutaric	124	2
L-Arabinose	64	2	*n*-Butyl	102	2	Malonic	88	2
			tert-Amyl	100	2	Azelaic	80	2
Hexoses			*n*-Amyl	99	2	Adipic	70	2
			iso-Butyl	96	2	Oxalic	20	1
D-Fructose	1855	18	*sec*-Butyl	95	2	Malic	234	3
Glucose	1521	16	*tert*-Butyl	50		Aconitic	162	3
D-Mannose	1415	14				Itaconic	158	3
			Polyhydric alcohols			Fumaric	151	2
D-Fructose, M/20	1033	11				Maleic	120	2
D-Galactose	945	9	Glycerol	1369	14	*m*-Tartaric	97	2
Gluctose, M/20	663	7	Mannitol	729	6	Citric	413	4
D-Galactose, M/20	235	3	Inositol	572	6			
L-Sorbose	191	3	Sorbitol	358	5	Salts		
L-Sorbose, M/2	68	2	Adonitol	308	4			
			m-Erythritol	170	3	Sodium succinate	115	2
Disaccharides			Dulcitol, M/5	119	2	Sodium citrate	105	2
			Dulcitol	108	2	Sodium lactate	115	2
Sucrose	2218	24	Arabitol	107	2	Sodium malonate	99	2
Sucrose, M/5	2141	23	*m*-Erythritol, M/2	86	2			
Maltose	2040	17	*penta*-Erythritol,					
Sucrose, M	2010	22	M/2	51	1			
Trehalose	1864	21	M/10	40	1			
Maltose, M/20	1668	16						
Sucrose, M/2	1624	20	Glycols					
Sucrose, 2M	1516	16						
Sucrose, M/20	1506	14	Propylene	172	3			
Melibiose	1237	12	Diethylene	160	2			
Sucrose, M/40	382	4	Ethylene	124	2			
Lactose	179	3	Dipropylene	60	2			
Lactose, M/2	153	2						
Lactose, M/20	100	2						
Cellobiose	84	2						
Cellobiose, M/2	40	1						

TABLE I—*Continued*

	A	B		A	B
Amino acids			Miscellaneous		
Glycine	202	3	Yeast-sucrose, equal parts, dry	2074	24
DL-Methionine	195	3	alpha-Methylglucoside	639	6
L-Glutamic acid	124	2	Yeast, fresh 2% suspension	165	3
DL-Aspartic acid	122	2	Parenamine, 1% (proprietary casein hydrolysate)	147	2
DL-Alanine	108	2			
Beta alanine	108	2	Amygdalin	139	2
L-Cystine (sat. sol.)	102	2	Yeast, fresh dry	128	2
L-Cysteine	101	2	Catechol	126	2
DL-Glutamic acid	101	2	Albumin, 1%	117	2
DL-Threonine	101	2	Lecithin, 1%	116	2
L-Arginine	95	2	Charcoal, dry	107	2
DL-Phenylalanine	93	2	Glucosamine	106	2
L-Histidine	89	2	Casein, dry	106	2
DL-Isoleucine	72	2	Gulonic lactone, 4%	105	2
L-Lysine	71	2	Magnesium hexosediphosphate	104	2
L-Proline	70	2	Glucoheptonic lactone, 4%	100	2
L-Leucine (sat. sol.)	67	2	D-Galacturonic acid	98	2
L-Hydroxyproline	66	2	Xylan (sat. sol.)	94	2
DL-Tryptophane (sat. sol.)	63	2	Sucrose acetate	93	2
L-Tryptophane (sat. sol.)	62	2	Mucic acid	90	2
L-Tryosine (sat. sol.)	57	2	Calcium glucoheptonate, 4%	84	2
DL-Leucine (sat. sol.)	55	2	Nucleic acid (sat. sol.)	83	2
DL-Norleucine	55	2	Sodium nucleate, 1%	82	2
DL-Serine	51	1	Yeast, dried, suspension	80	2
DL-Valine	51	1	Milk, powdered	78	2
			Yeast, dried	64	2
			Starch, Lintner, dry	45	1
			Xanthine (sat. sol.)	15	1
			Guanine	13	1
			Uracil	13	1

include not only substances not utilized when ingested, but those which might be utilized somewhat, were they not also slightly repellent so that the flies do not drink the solutions.

Group 2. Substances which are utilized by Drosophila, shown by scores higher than that of water. This group includes anything which prolonged the life of the flies in any degree, from such poor nutrients as xylose to the best of the higher sugars. Sugars, particularly the mono-, di-, and trisaccharides, lead in this group, but moderately good results were obtained with dextrin, glycerol, mannitol, inositol, and alpha-methylglucoside. Some prolongation of life was obtained with starch, glycogen, sorbitol, adonitol, and with butyric, acetic, lactic, succinic, malic, and citric acids. The only amino acids showing any usefulness were methionine and glycine. A few other substances, such as ethyl alcohol, propylene and diethylene glycol, aconitic and itaconic acids, were doubtful. Proteins alone, e.g. albumin, were of no value, nor were such products as casein, yeast, or milk. The low values obtained with dry yeast (64) and starch (45) prompted a test with an inert powder. Charcoal was selected, and the relatively high score (107) suggests that there is something definitely harmful in dry starch and yeast, but whether its nature is

physical or chemical has not yet been ascertained. Dry yeast mixed with an equal amount of powdered sugar, on the other hand, makes an excellent food, giving a score of 2074.

In order to obtain a more exact comparison of nutritive value among some of the commoner sugars, seven were tested under identical conditions. The molarities of the solutions were chosen to equate the mono- and disaccharides with respect to weight per unit volume. Lactose, M/20, and xylose, M/10, showed no nutritive value, and galactose, M/10, very little. The other sugars were, in order of increasing nutritive value: glucose, M/10, 1375; sucrose, M/20, 1440; maltose, M/20, 1720; fructose, M/10, 1833. These scores and the curves of Figure 1 show there was little variation in this group, also that the results were nearly the same as those shown in Table I for the larger series of experiments.

The longevity of flies fed on di- and trisaccharides was compared, under identical conditions, with that of flies fed on the constituent monosaccharides. Table II

TABLE II

A comparison of some di- and trisaccharides with their hexose constituents. Each pair was run with flies from the same batch, under identical temperature conditions.

Substance	Conc.	Score	Substance	Conc.	Score
Sucrose	M/20	1455	Raffinose	M/20	1460
Fructose Glucose	M/20 M/20	1421	Fructose Glucose Galactose	M/20 M/20 M/20	1492
Maltose	M/20	1466			
Glucose	M/10	1363	Melezitose	M/20	1257
Trehalose	M/20	1064	Glucose Fructose	M/10 M/20	1285
Glucose	M/10	1285			

shows that there was little difference in the results, a mixture of fructose and glucose being as good as an equivalent amount of sucrose, etc.

Larvae. The results obtained in rearing sterile larvae on yeast and on yeast-sugar mixtures are given in Table IV. No significant difference was found in the number of flies produced by the three sugar media. A significant difference was found when adequate amounts of yeast were supplied, and an increase in the amount of sugar might have increased the yield. Since the object of the experiment was to differentiate among the sugars, if possible, by putting the larvae into somewhat unfavorable conditions, this was not done. Flies consuming fructose developed more rapidly than those on sucrose and glucose, though less rapidly than those having a full yeast diet.

Group 3. Substances which have low scores, and are therefore toxic or repellent. Flies in a bottle having a layer of agar live almost as long as if they are supplied with drinking water. Substances which are merely repellent will, therefore, be difficult to separate from those which are nutritionally inert. Toxic sub-

stances should give much lower scores and be accordingly easier to single out. Guanine, for example, is clearly toxic. Variations in toxicity and in the flies themselves naturally militate against any sharp distinction, so that further experiments were performed to bring out hidden differences. The difference between toxic and repellent substances can sometimes be demonstrated readily by offering a questionable solution alone and in combination with a separate vial of water. Rhamnose alone, for example, gave a score of 68, but when the flies were offered

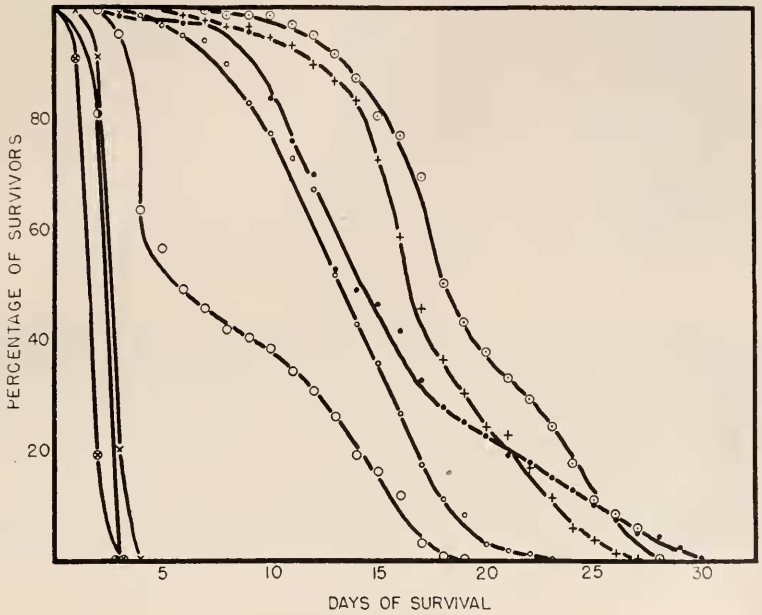

FIGURE 1. The duration of life of adult fruit flies fed solutions of various sugars. Lactose, M/20, ⊗; water, ◑; xylose, M/10, ×; galactose, M/10, ○; glucose, M/10, ○; sucrose, M/20, ●; maltose, M/20, +; fructose, M/10, ⊙.

an additional vial of water, the score rose to 100. No discrimination was evidenced, and presumably the flies lived longer because they drank less of the rhamnose solution. When repellency is suspected, however, something must be used to insure the ingestion of the solution. Vogel (1931) used sucrose solution, and a M/40 solution of sucrose was found useful in these experiments. Testing a large number of flies with this solution alone gave a score of 382. Table III shows how the results differed when various substances were added to it. Dulcitol alone is seemingly inert in M/10 solution, but when M/40 sucrose is added, the flies live longer than in sugar alone (score 508). Isoleucine is inert either way. D-Arabinose, on the other hand, prolongs life slightly when alone but shortens it when added to the sucrose solution, a puzzling result, to be sure. Sorbose would seem to be toxic either alone or in sucrose solutions, as do tartaric acid, norleucine and histidine, while valine, which is toxic when alone, can probably be detoxified when sucrose is present.

Table III

The effect of certain substances on Drosophila when dissolved in water and in M/40 sucrose. Each pair run under identical conditions.

Substance	Conc.	Score	
		In water	In M/40 sucrose
Cellobiose	M/10	84	396
Dulcitol	M/5	119	508
D-Arabinose	M/5	170	162
L-Sorbose	M/2	68	285
M-Tartaric acid	M/5	102	124
D-Tartaric acid	M/5	80	115
DL-Norleucine	M/10	20	83
DL-Valine	M/10	24	353
DL-Isoleucine	M/10	111	360
L-Histidine	M/10	93	203

Discussion

As noted above, the question of what sugars can be utilized by insects has been investigated for several species. The results in hand for the adult and larval bee, the adult blowfly, and for the adult fruit flies *Anastrepha* and *Drosophila,* indicate almost identical abilities to utilize sugars, as nearly as the data are comparable. The really clear cut differences reported are as follows: mannose is used by *Calliphora, Anastrepha* and *Drosophila,* but not by the bee. Indeed von Frisch (1934) and Staudenmayer (1939) have reported a specific toxicity of mannose for the bee. Melibiose, dextrin, starch, and glycerol are not used by adult bees, but

Table IV

The development of sterile Drosophila larvae on low yeast, low yeast plus sugars, and adequate yeast diets.

Medium	Number of eggs (36/vial)	Number of pupae	Mean number of pupae per vial	Difference divided by prob. error of difference	Number of adults	Mean number of adults per vial	Difference divided by prob. error of difference	Mean number of days for emergence of all flies
0.5% yeast	252	73	10.3±2.9*	2.0	67	9.6±3.3*	2.0	20.5±3.4*
0.5% yeast 0.5% glucose	180	106	21.2±4.1	0.8	102	20.4±4.3	0.6	21.0±1.7
0.5% yeast 0.5% sucrose	540	371	28.5±2.3	2.0	353	27.1±2.3	1.4	21.5±1.3
0.5% yeast 0.5% fructose	216	183	30.5±1.0	3.0	178	29.7±1.8	4.5	16.2±3.7
2.0% yeast	72	70	35.0±0.9		70	35.0±0.9		12.0±0.0

* Probable error.

are by *Calliphora* and *Drosophila*. Inositol is utilized by *Drosophila*, but not by the others, and arabinose is used by *Apis* alone. There are other differences reported, such as the use of fucose by *Drosophila* and not by other forms, but the degree of utilization is so small that the difference is unimportant. The present experiments do show, however, that no substance should be judged inert until it has been tested in several concentrations, e.g. xylose is very poor in M/10 or less, but definitely useful in M/2. Also, substances should not be finally classified as useless or toxic unless they are offered in such form that ingestion is certain. Dulcitol, for example, is apparently inert for *Drosophila* when given alone, even up to M/5, yet when it is dissolved in M/40 sucrose, the flies live longer. The comments of Vogel (1931), Haslinger (1935) and Fraenkel (1940) are also pertinent to this point.

The ability of *Calliphora* and *Drosophila* to utilize glycogen and starch is clear, although it is much less than the ability to utilize sugars. The danger of using a partially hydrolyzed starch should be noted. *Drosophila* fed Lintner's soluble starch, one per cent, gave a score of 625, whereas sugar-free corn starch scored only 334. Reducing sugar was readily demonstrated in the soluble starch, which may account for the partial development of *Aedes* larvae reported by Hinman (1933).

The question of which sugar is best, which was raised by Bertholf (1927), is, perhaps, one applicable only to the individual species. It is further complicated by the variety of standards adopted by various investigators. Yet it is interesting to note that the "physiological sugar," glucose, is consistently poorer than others, being rated second by Phillips, third by Baker and Fraenkel, and fourth by Bertholf and in the present experiments, when only sucrose, maltose, glucose, and fructose are considered. Fructose, on the other hand, is rated first by Phillips, equal to sucrose by Fraenkel, second to sucrose by Bertholf, and in the present experiments it was superior to the others. Indeed, a comparison of scores for M/10 fructose and M/20 raffinose indicates that fructose is superior to the trisaccharides also. Sucrose is at or near the top in all.

The curve for galactose in Figure 1 is also of some interest. The initial mortality was so heavy that it suggested reduced powers for utilization of galactose, or greater power of mobilizing enzymes, on the part of one of the two portions of the population. A repetition of the experiment yielded similar results. The basis of the variability is not known but it will be investigated.

Partial successes were obtained with the substances regarded as intermediate products of carbohydrate metabolism. None of these was utilized by *Calliphora* (Fraenkel); *Drosophila*, however, survives a short time on citric, malic, succinic, lactic, butyric, and acetic acids, and possibly also on aconitic, itaconic, fumaric, and pimelic acids, although these are on the borderline. Since there is such close agreement in other respects, these data suggest that the blowfly might be able to metabolize the compounds in question, a possibility which Fraenkel has pointed out. In an experiment in which the present technique was used with *Lucilia sericata*, the flies died about as rapidly when offered M/10 citric acid or dry citric acid as they did when offered water alone. *Calliphora* was not available for this test, but the results with *Lucilia* suggest that if blowflies are able to metabolize any of the intermediates, some other means must be employed for introduction of the material.

According to Weidenhagen (1931), and the somewhat modified point of view

of Pigman (1944), all carbohydrates can be split by a small number of enzymes. With Weidenhagen's work in mind, Fraenkel concludes that only two enzymes, an alpha-glucosidase and an alpha-galactosidase, need exist in *Calliphora* to split all the carbohydrates that the blowfly utilizes. *Drosophila* evidently depends largely on the same two, but may have in addition a fructofuranosidase, which would be needed to utilize inulin, and could also act on sucrose. An amylase, too, must be present to split starch and glycogen.

While the longevity of the fruit fly on sugar alone may seem remarkable (50 per cent survival up to four weeks), the much greater longevity on the standard culture medium which furnishes carbohydrate directly and protein and accessory factors from the yeasts growing on the medium suggests that the addition of traces of other substances to the sugar solution might increase survival greatly. A further point on longevity is that the present method is not calculated to produce the longest lived flies. According to Pearl, Miner and Parker (1927), the maximum longevity of *Drosophila* is found in relatively crowded populations, about 50 flies in a 30 ml. vial having given best results in their experiments.

Summary

1. *Drosophila melanogaster* can survive for varying periods on pure solutions of many compounds, including sugars, polysaccharides, polyhydric alcohols, aliphatic acids, etc.

2. In equivalent solutions, the order of usefulness of some common sugars was found to be: fructose > maltose > sucrose > glucose > galactose > xylose > lactose.

3. There is no significant difference in life span between flies fed on disaccharides and their constituent monosaccharides.

4. Doubtful sugars can usually be resolved into toxic, repellent, or slightly useful substances by offering them in dilute sucrose solutions.

5. On a sterile, "starvation" diet, larvae develop better on fructose than on glucose.

6. On the basis of survival when fed pure substances, *Drosophila* seems to possess alpha-glucosidase, alpha-galactosidase, beta-fructofuranosidase and amylase.

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